OBSERVATIONS OF REACTION FIBERS IN LEAVES OF DICOTYLEDONS

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HALLÉ, OLDEMAN, AND TOMLINSON (1978) have discussed the transference of function between compound leaves and plagiotropic branches in the context of tree architecture. In trees conforming to Cook's model (see Hallé, Oldeman, & Tomlinson, 1978), plagiotropic branches resemble compound leaves in their determinate growth and their periodic abscission. Conversely, certain trees (primarily in the Meliaceae) have compound leaves that behave like plagiotropic branches. The rachis of such a leaf grows indeterminately, sometimes reaching lengths of up to 6 m (Sinia, cited in Hallé, Oldeman, & Tomlinson, 1978). The leaves persist on the tree for several years, in some species even forming growth rings in the extensive secondary xylem of the rachis (Skutch, 1946). The present study was stimulated by the observation of another branchlike feature of these leaves—the presence of reaction wood in the rachis. This paper describes reaction fibers in dicotyledonous leaves and presents speculations on the extent to which their function in leaves is similar to their known function in branches.

Reaction fibers have been extensively studied in the secondary xylem of roots and shoots and have been found in primary phloem (Scurfield, 1964) and nonvascular tissue (Staff, 1974). There is strong circumstantial evidence that individual reaction fibers contract during development, generating a contractile force in the axis (Wardrop, 1964). Thus, the distribution of reaction fibers in an axis correlates positively with the distribution of contractile forces in the axis. The contraction associated with the presence of reaction fibers in shoots assists in secondary orientation, and in aerial roots of *Ficus benjamina* L. aids in anchoring the plant (Fisher & Stevenson, 1981; Wardrop, 1964; Wardrop, Tomlinson, & Zimmermann, 1964). Reaction-fiber contraction is probably a consequence of the characteristic structure of the reaction-fiber wall. Scurfield (1973) has proposed a mechanism for this contraction based on the relationship between cellulose microfibril orientation in the layers of the fiber wall and the differential lignification of these layers.

Although the contractile forces involved in secondary orientation are often associated with the presence of reaction fibers, this is not always the case. There are many plant families (e.g., in the order Malvales; Kucera & Philipson, 1977) in which reaction fibers have never been observed. In their investigation of the role of reaction fibers in tree architecture, Fisher and Stevenson (1981) found that pronounced changes in the orientation of woody branches, which are characteristic of certain architectural models, occur in

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many tree species that lack reaction fibers. Other modifications of the secondary xylem and/or secondary phloem that correlated with the observed changes in woody-branch orientation were found in most of these species. Thus, the reaction fiber is only one anatomic feature associated with contractile forces and secondary orientation in plants.

Despite the extensive study of reaction fibers, there is apparently no previous account of their occurrence in dicotyledonous leaves. Although Patel (1964), writing on gelatinous fibers in root wood, made brief mention of similar fibers in the petiole of *Cercis* and the leaf rachis of *Caragana,* he gave no details of their origin, distribution, or structure. Extra-xylary reaction fibers have been found in the leaves of the Australian monocotyledon *Xanthorrhoea australis* R. Br. (Xanthorrhoeaceae) by Staff (1974); this is the only known occurrence of reaction fibers in monocotyledons.

Reaction fibers in dicotyledonous leaves could be identified because of their structural similarity to reaction fibers in stems of the same plant. Speculations on the function of these fibers in leaves were based on the observed arrangement of the fibers in the leaf axis; the assumption was made that individual reaction fibers contract by virtue of their structure. The observations presented in this paper indicate that in certain species reaction fibers in leaves appear to function in the same manner as they do in branches and their presence may be correlated with an over-all branchlike appearance and behavior of the leaf; thus, the transference of function between leaf and branch appears to be an anatomic as well as a morphological phenomenon. In the leaves of other species, however, reaction fibers do not function as they do in branches, and there is no obvious modification of the leaf into a branchlike structure; a unique function for reaction fibers in these axes is suggested.

MATERIALS AND METHODS

The species examined are listed in TABLE 1. Transverse sections were cut by hand at various levels of the axes of fresh leaves, and the sections were stained in phloroglucinol and concentrated HCl. Sections were examined under the microscope in normal and polarized light.

Four species (*Rhus typhina* L., *Wisteria sinensis* Sweet, *Cercis canadensis* L., and *Robinia pseudoacacia* L.) were selected for more detailed study. Within a single plant of each species, the reaction fibers in the leaves were compared with those occurring in a branch and were contrasted with fibers in a vertical shoot. Material was fixed in FAA, embedded in paraffin, and sectioned on a rotary microtome at 7 and 10 μm. Sections were stained with safranin and counterstained with chlorazol black E by a method modified from Robards and Purvis (1964). Some sections were left unstained for observation under polarized light.

Xylem reaction fibers were identified by the presence of a so-called gelatinous or S(G) layer in the secondary wall of the fiber; this unique layer can be distinguished from the first (S_1), second (S_2), and third (S_3) layers of normal xylem fibers. The S(G) layer is typically the innermost layer of the

TABLE 1. **Taxa investigated.**

TAXON	REACTION FIBERS		LEAF TYPE
	Xylem	Phloem	
Anacardiaceae			
Rhus typhina L.	+	+	Compound
Juglandaceae			
Juglans cinerea L.	−	−	Compound
Leguminosae			
Caragana arborescens Lam.	−	+	Compound
Cercis canadensis L.	+	+	Simple
Delonix regia Bojer	+	+	Compound
Gleditsia triacanthos L.	+	+	Compound
Inga paterne Harms	+	+	Compound
Robinia pseudoacacia L.	+	+	Compound
Wisteria sinensis Sweet	+	+	Compound
Magnoliaceae			
Liriodendron tulipifera L.	−	−	Simple
Meliaceae			
Azadirachta indica Juss.	−	−	Compound
Carapa guianensis Aublet	+	+	Compound
Cedrela fissilis Vell.	+	?	Compound
Guarea glabra Vahl	+	?	Compound
Swietenia mahagani (L.) Jacq.	−	−	Compound
Oleaceae			
Fraxinus americana L.	−	−	Compound
Rosaceae			
Crataegus sp.	−	−	Simple
Rutaceae			
Phellodendron sp.	−	−	Compound
Simaroubaceae			
Ailanthus altissima (Miller) Swingle	−	−	Compound
Tiliaceae			
Tilia cordata Miller	−	−	Simple
Ulmaceae			
Ulmus americana L.	−	−	Simple

secondary wall and is either a second ($S_2(G)$) or third ($S_3(G)$) layer of the wall. The S(G) layer is unlignified and has a high cellulose content; thus it is unstained in a phloroglucinol/HCl stain and stains black in chlorazol black E. Because cellulose microfibrils in the S(G) layer run axially, the layer is isotropic or slightly birefringent when viewed in transverse section under polarized light (Wardrop, 1964). The S(G) layer is weakly adherent to the adjacent layer, often causing it to pull away in sectioning. A well-developed S(G) layer may be so thick as to occlude the cell lumen.

Phloem reaction fibers were identified by the presence of a secondary wall layer identical in staining, position, adherence, and isotropy to the S(G) layer of xylem reaction fibers. The structural similarity between phloem fibers with this layer and xylem reaction fibers presumably reflects similar contractile

properties and justifies classification of these phloem fibers as reaction fibers. Although the S(G) layer was originally used to denote reference to the "gelatinous" layer of the xylem reaction fibers, Staff (1974) has applied the term to analogous layers in extra-xylary fibers in his description of primary reaction fibers in *Xanthorrhoea australis;* this precedent will be followed in referring to the S(G) layer of phloem reaction fibers.

OBSERVATIONS

GENERAL. TABLE 1 indicates the diversity of taxa in which xylem and phloem reaction fibers were found in the leaves. Although leaf reaction fibers were generally observed in species with large compound leaves, they were not always found in such species (e.g., *Ailanthus altissima* (Miller) Swingle). The seemingly common occurrence of reaction fibers in leaves of the Meliaceae and Leguminosae suggests that, at one level, the presence of leaf reaction fibers correlates more closely with taxonomic grouping than with compound leaf structure or leaf size.

Within the Meliaceae and Leguminosae, however, correlations were observed between leaf size and reaction fiber distribution in the leaf axis. In the Meliaceae the small (rachis < 25 cm) compound leaves of *Swietenia mahagani* (L.) Jacq. and *Azadirachta indica* Juss. lack reaction fibers, whereas the much larger (rachis > 40 cm) compound leaves of *Guarea glabra* Vahl, *Carapa guianensis* Aublet, and *Cedrela fissilis* Vell. have them (see TABLE 1). In these larger compound leaves, reaction fibers (whether in the xylem or the primary phloem) were consistently found on the side of the rachis facing upward with respect to gravity. (This upper side is not always the same as the morphologically adaxial surface of the leaf axis.) Reaction fibers uppermost in the rachis were also observed in *Rhus typhina* (FIGURE 1, A).

In the Leguminosae both large- and small-leaved species have leaf reaction fibers. The distribution of these fibers in the leaf axis, however, varies according to the size of the leaf. The large (rachis 15–25 cm) compound leaves of the tropical species *Delonix regia* Bojer and *Inga paterne* Harms generally have leaf reaction fibers toward the upper surface of the rachis, as do the large leaves of the Meliaceae and *Rhus typhina*. In the smaller-leaved temperate leguminosae (*Wisteria sinensis, Caragana arborescens* Lam., *Gleditsia triacanthos* L., *Cercis canadensis, Robinia pseudoacacia*) there was no consistent distribution of the leaf reaction fibers with respect to either gravity or the adaxial surface of the leaf axis. FIGURE 1, B shows them scattered above and below with respect to gravity in a rachis of *Wisteria sinensis*. In other small-leaved species they were found in a wide sector of the leaf axis at right angles to the force of gravity, and they occasionally occurred around the entire circumference.

Certain aspects of reaction-fiber distribution in leaves were consistent in all species. Where xylem and phloem reaction fibers occurred together, they were always found on the same side of the rachis, with the phloem reaction fibers occupying the wider sector (see FIGURE 1, A, B). Phloem reaction fibers were always found throughout the length of the rachis; xylem reaction

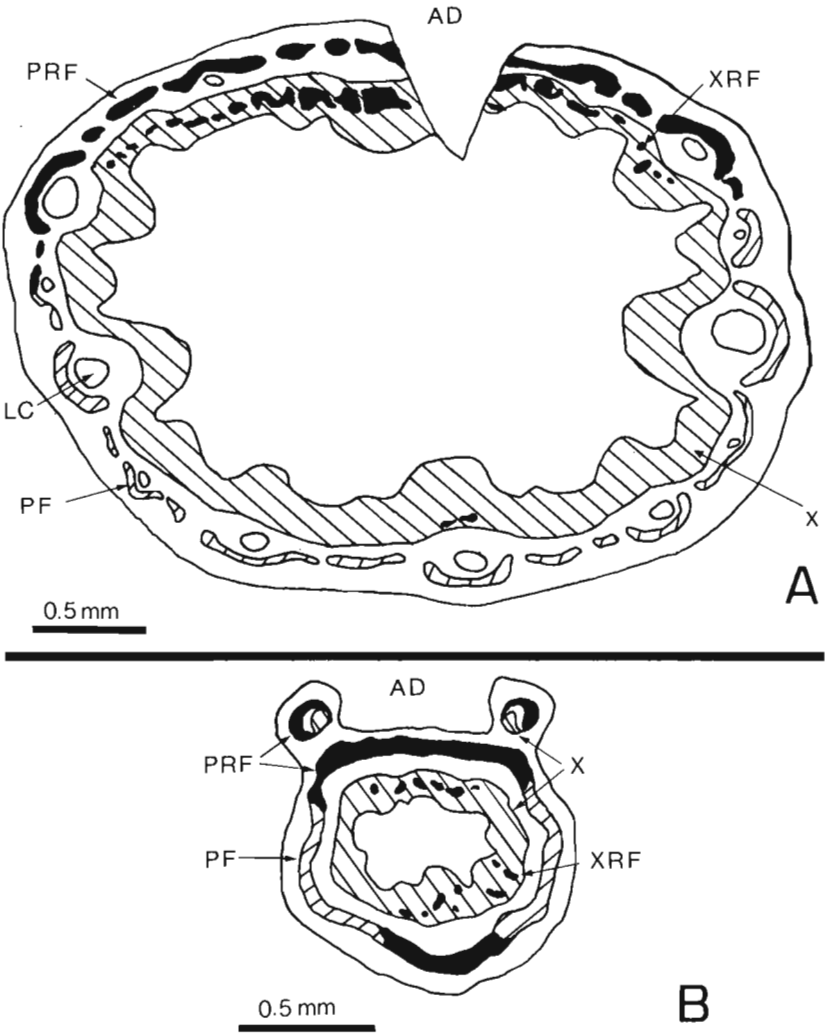


FIGURE 1. Reaction-fiber distribution in leaf axes: A, *Rhus typhina,* proximal section of rachis, notch made to mark upper side prior to sectioning; B, *Wisteria sinensis,* proximal section of rachis. AD = adaxial side of axis (in these examples corresponding with uppermost side of rachis with respect to gravity), PF = primary phloem fibers, PRF = phloem reaction fibers, X = xylem, XRF = xylem reaction fibers, LC = latex canal.

fibers were seen only in the proximal half. Reaction fibers were absent from the pulvinus in all species examined.

RHUS TYPHINA, WISTERIA SINENSIS, ROBINIA PSEUDOACACIA, CERCIS CANADENSIS. Xylem reaction fibers in stems of these species showed similar distributions.

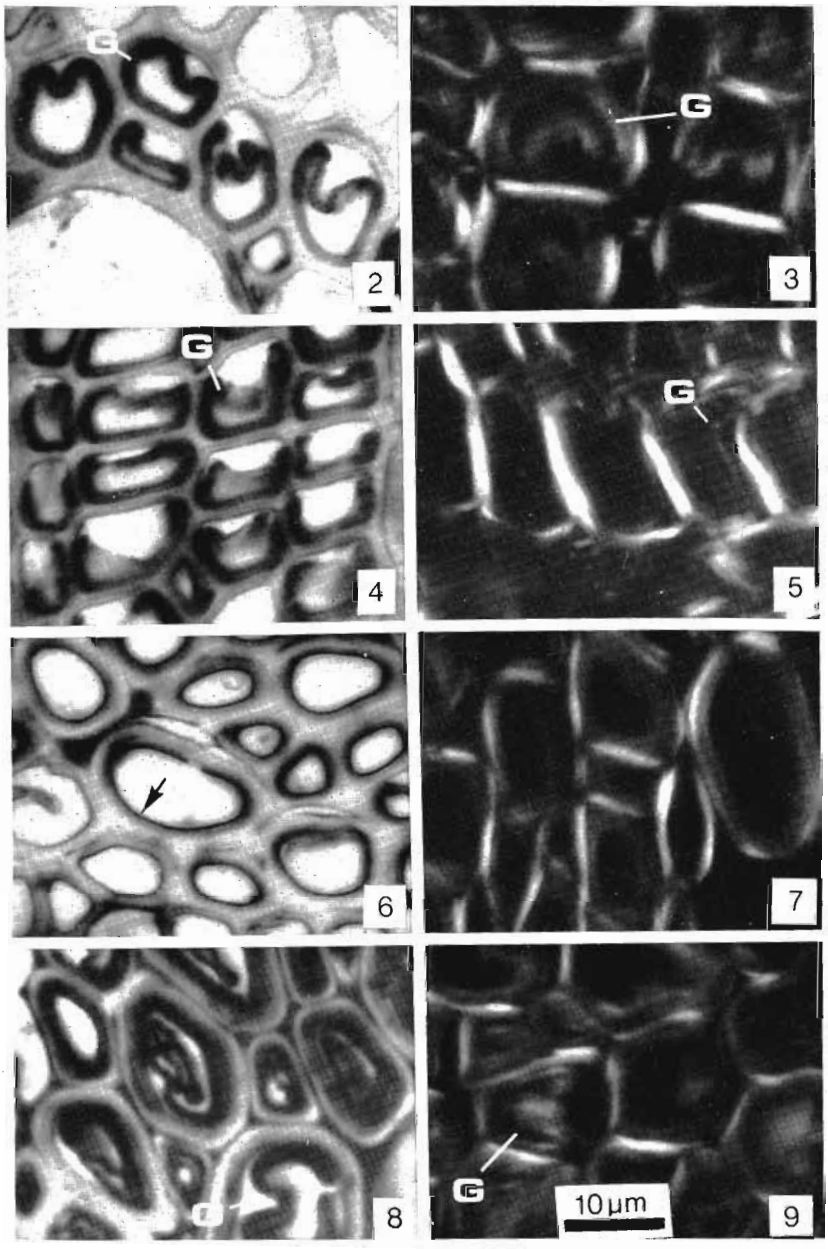
Inclined or horizontal branches had xylem reaction fibers in thick bands uppermost in the axis. Smaller numbers of reaction fibers were found in the xylem of vertical shoots either in a single unilateral band or in bands that overlap radially in wood of different ages. Phloem reaction fibers, although present in the leaves of all four species, were found only in the stems of *Rhus typhina*.

Xylem reaction fibers in the leaves and stems of these four species had the same wall structure. FIGURES 2–5, 10–13, and 20–23 show the S_1-S_2-S_3(G) layering of xylem reaction fibers in leaves and stems. Occasional reaction fibers with an S_1-S_2(G) structure were seen in both organs. The birefringence of the S(G) layer varied from slight in the *Rhus* stem (FIGURE 5) and the *Robinia* leaf (FIGURE 11) to nearly as bright as that of the S_2 layer in the *Wisteria* leaf (FIGURE 21). Scurfield and Wardrop (1962) found that in secondary xylem reaction fibers of *Tristania conferta* R. Br. and *Grevillea robusta* A. Cunn., the S(G) layer is birefringent early in development and loses this birefringence as the layer matures. Perhaps the variation in S(G) birefringence observed in the present study has the same explanation. The diameter of reaction fibers varies considerably (compare FIGURES 10 and 22) but does not appear to be correlated with whether the fiber is in a leaf or a stem.

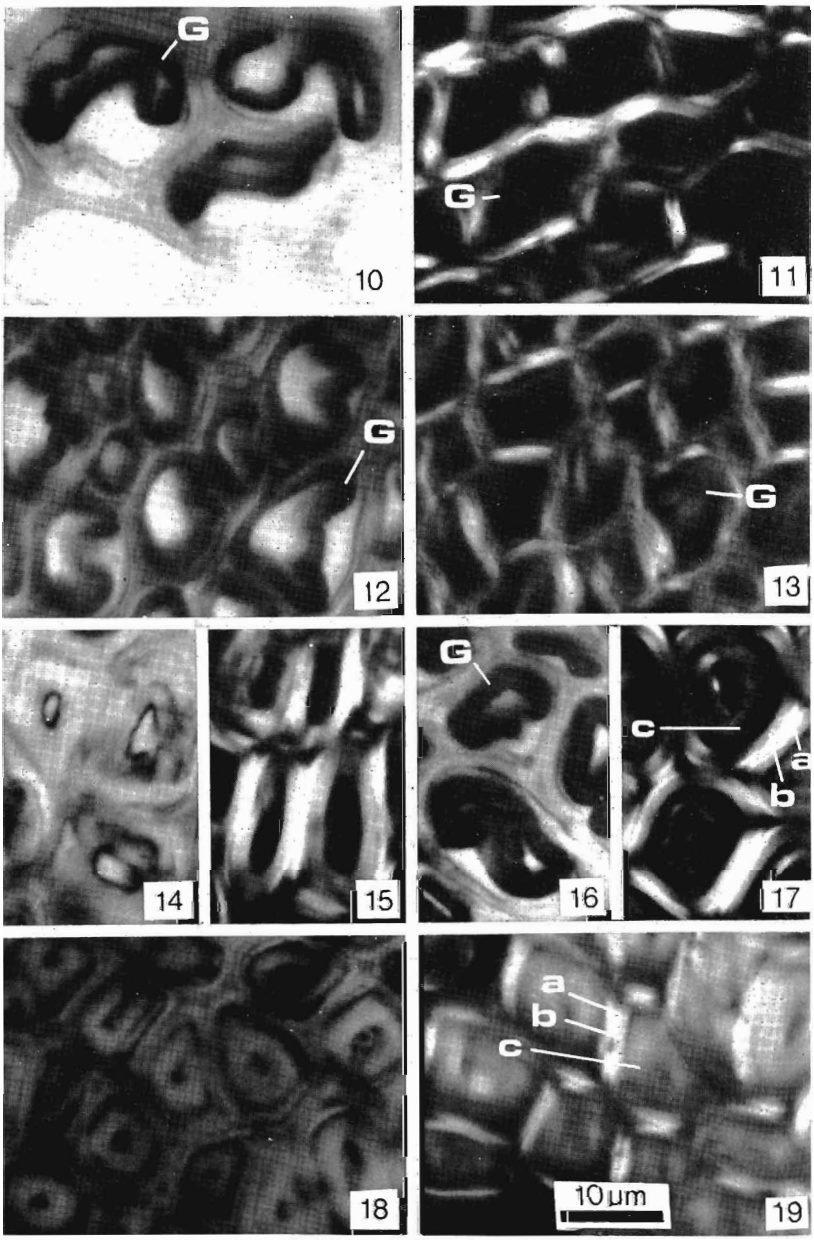
Phloem reaction fibers were primary in origin in these species. Like xylem reaction fibers, they had an S_1-S_2-S_3(G) wall structure (FIGURES 8, 9, 16, 17, 25, 26). The similarity between xylem and phloem reaction fibers is indicated in a comparison of *Robinia* phloem reaction fibers (FIGURES 16, 17) with *Wisteria* xylem reaction fibers (FIGURE 23). Although in the four species investigated phloem reaction fibers generally had larger diameters than xylem reaction fibers, in some cases (e.g., *Rhus* leaf, FIGURE 2) the diameters were equal. As in xylem reaction fibers, the birefringence of the S(G) layer in phloem reaction fibers varied somewhat, perhaps related to fiber development. Some of this birefringence could be due to the rearrangement of the S(G) layer during preparation.

FURTHER OBSERVATIONS OF PRIMARY PHLOEM REACTION FIBERS. Because primary phloem reaction fibers have never been reported from leaves and have only rarely been studied in stems, their occurrence in *Rhus typhina, Wisteria sinensis, Robinia pseudoacacia, and Cercis canadensis* will be described in more detail. In *Rhus typhina,* primary phloem reaction fibers with an identical structure were present in both stems and leaves (FIGURES 8, 9). The two convoluted, black-staining layers evident in FIGURE 8 are typical. Because both layers have the same weak birefringence indicating a common, near-axial microfibril orientation, they are probably laminations of a single S_3(G) layer. FIGURES 6 and 7 show nonreaction phloem fibers from the underside of a rachis. Although they lack the thick, convoluted S(G) layer of the reaction fibers, they have a thin, adherent, isotropic, black-staining layer (ar-

FIGURES 2–9. *Rhus typhina,* transverse sections. In each pair of illustrations, left photograph shows section stained in chlorazol black in normal light, right shows unstained section between crossed polarizers. G = S(G) layer of reaction fibers. 2, 3,



xylem reaction fibers in rachis; 4, 5, xylem reaction fibers in stem; 6, 7, nonreaction phloem fibers in rachis (arrow in 6 indicates narrow black layer apparently homologous with S(G) layer in reaction phloem fibers); 8, 9, reaction phloem fibers in rachis.



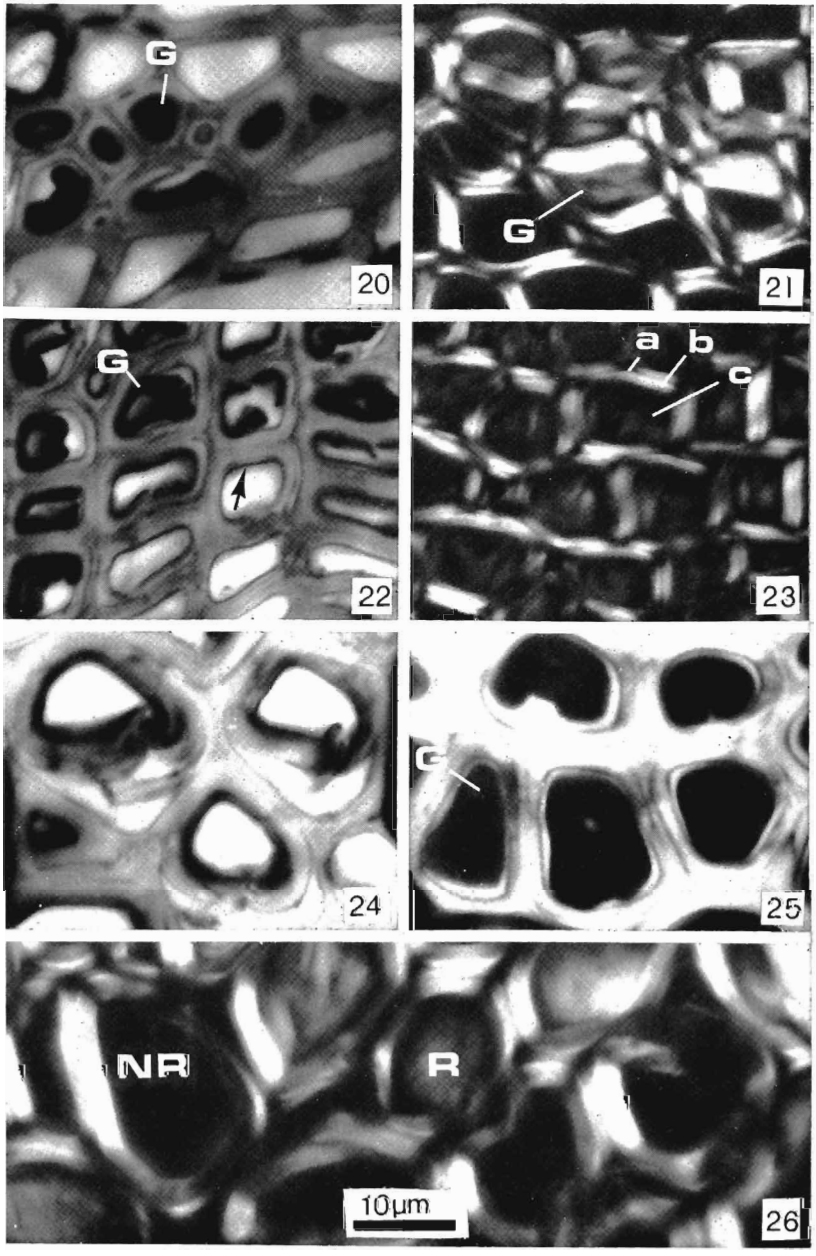
FIGURES 10–19. *Robinia pseudoacacia*, transverse sections. In each pair of illustrations, left photograph shows section stained in chlorazol black in normal light, right shows unstained section between crossed polarizers. G = S(G) layer of reaction fibers. 10, 11, xylem reaction fibers in rachis; 12, 13, xylem reaction fibers in stem;

row, FIGURE 6) that appears from its position and birefringence to be homologous with an S(G) layer. This apparent homology is best seen on the side of the rachis where the two fiber types intergrade. An analogous situation in xylem reaction fibers is shown in FIGURE 22. The arrow indicates a narrow, black layer that is probably homologous to the thick S(G) layers of adjacent fibers.

In a study of primary phloem reaction fibers in stems of *Lagunaria pattersonii* G. Don, Scurfield (1964) found that phloem reaction fibers occurring uppermost in inclined branches differed from nonreaction phloem fibers in the underside of the branch only in the greater development within individual reaction fibers of an isotropic, unlignified layer. This situation is identical to that in *Rhus typhina*. Scurfield interpreted this to indicate that both reaction and nonreaction phloem fibers conform to the same developmental plan: the nonreaction fiber with its narrow isotropic layer represents an immature state, and the reaction fiber with its thickened S(G) layer represents the mature one. Scurfield suggested that the phloem fibers uppermost in an inclined branch at a given level develop more rapidly than the phloem fibers in the underside of the branch at the same level. This hypothesis was supported by the fact that all primary phloem fibers in the older stems of *Lagunaria pattersonii* are reaction fibers. Since this is also true of old stems in *Rhus typhina*, Scurfield's explanation of the origin of phloem reaction fibers in *Lagunaria pattersonii* may also apply to these primary fibers in *Rhus typhina*.

In the three leguminous species (*Cercis canadensis, Robinia pseudoacacia,* and *Wisteria sinensis*) primary phloem reaction fibers were found only in leaves. Within the leaf the relation of reaction to nonreaction fibers was the same as in *Rhus typhina:* the two fiber types appear to differ only in the degree of development of an S_3 layer (FIGURES 14–17, 24–26). In the leaf the difference between reaction and nonreaction phloem fibers may also be interpreted in terms of rates of development. Primary phloem fibers in the stem, however, are not reaction fibers and apparently develop differently than those in the leaves. FIGURES 14–19 show the difference between primary phloem fibers in the stem and leaf of *Robinia pseudoacacia*. The S_3 layer in the leaf appears to be a G layer of varying thickness that stains black in chlorazol black (FIGURES 14–17), whereas the corresponding layer in the stem is consistently thick and birefringent and stains gray in the same stain (FIGURES 18, 19). Secondary phloem fibers were only sporadically present in the rather small (1–2 cm in diameter) stems examined and were absent from the leaves of all four species. Secondary phloem fibers do occur in the leaf rachis of some Meliaceae (J. Fisher, pers. comm.).

14, 15, nonreaction phloem fibers in rachis; 16, 17, reaction phloem fibers in rachis (in 17, a = very birefringent S_1 layer, b = moderately birefringent S_2 layer, c = weakly and unevenly birefringent S_3(G) layer); 18, 19, phloem fibers in stem (in 19, a = S_1 layer, b = S_2 layer, c = S_3 layer). Note difference in wall structure (especially birefringence and form of S_3 layer) between stem phloem fibers in 14–17 and leaf phloem fibers in 18, 19.



FIGURES 20–26. Transverse sections. 20–23, *Wisteria sinensis:* 20, 21, xylem reaction fibers in rachis; 22, 23, xylem reaction fibers in stem (in 23, a = very birefringent S_1 layer, b = birefringent S_2 layer, c = weakly birefringent S_3(G) layer). 24–26, *Cercis canadensis,* petiole: 24, nonreaction phloem fibers; 25, reaction

DISCUSSION

The observation of xylem and phloem reaction fibers in leaves raises the question of how their functions compare in leaves and shoots. In this context observations concerning reaction-fiber distribution in leaves and shoots are relevant. In shoots examined in this study, reaction fibers were found where their contraction could assist either in holding branches at a given position or in maintaining the position of vertical axes. This is consistent with the general finding that stem reaction fibers function in secondary orientation. Orientation seems to be the function of reaction fibers in some leaves but not in others.

The consistent distribution of leaf reaction fibers uppermost in the rachis of the larger-leaved species in the Leguminosae and the Meliaceae, as well as in *Rhus typhina*, argues for an orientation function for leaf reaction fibers in these species; a branchlike distribution of reaction fibers is correlated with the maintenance of the horizontal position of the leaf. Although reaction fibers were absent from the pulvinus of these species, this area is sufficiently rigid and broad based in each species to provide a fixed support for the rachis. A rigid connection with the parent axis makes it possible for the reaction fibers in the rachis to aid in the horizontal positioning of the leaf.

The apparent participation of reaction fibers in the transference of function between leaf and branch in these large compound leaves is especially evident in *Guarea glabra* (Meliaceae). In this species the branchlike distribution of reaction fibers in the rachis is accompanied by other branchlike features of considerable secondary growth, indeterminate extension growth, and prolonged longevity. It is interesting to note that there are very few reaction fibers in the highly modified, leaflike branches of *Phyllanthus acidus* Skeels and *P. grandifolius* L. (Euphorbiaceae—pers. obs.).

In discussing the role of reaction fibers in the transference of function between leaf and branch, it is important to remember that not all branches and large compound leaves have reaction fibers. Reaction fibers were not found in the large leaves of *Ailanthus altissima* or *Juglans cinerea* L. (TABLE 1), and they appear to be absent from several woody plant families (Kucera & Philipson, 1977). In plants or parts of plant framework that lack reaction fibers, there can be other anatomic features that generate the contractile forces required to control secondary orientation (see Fisher & Stevenson, 1981). Reaction fibers represent a branchlike modification in leaves only if they are also present in the branches of the same plant.

In addition to assisting in the maintenance of leaf orientation with respect to gravity, reaction fibers in the larger, pinnately compound leaves of *Inga paterne* (Leguminosae) may have consequences for another aspect of leaf positioning. Due to the highly variable orientation of the parent axis, the adaxial surface of the rachis often faces as much as 90 to 180 degrees away

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phloem fibers; 26, nonreaction (NR) and reaction (R) phloem fibers. 20, 22, 24, 25, sections stained in chlorazol black, photographed in normal light; 21, 23, 26, unstained sections between crossed polarizers; G = S(G) layer in reaction fibers.

from its upward-facing surface. Between the rachis base and the first few leaflet nodes, however, the rachis is frequently twisted so that the adaxial and uppermost surfaces nearly coincide. This orientation results in the full display of leaflets to the sun. Throughout the twisted rachis, reaction fibers occur in the uppermost sector. This naturally suggests that reaction fibers may aid in maintaining the leaf at a given position with respect to gravity. However, the reaction fibers are distributed in a spiral opposite to that of the twist in the rachis. The contraction of reaction fibers distributed in this fashion may thus also aid in maintaining the twist. Developmental studies are needed to clarify whether the twist in the rachis is primary and is later reinforced by development of reaction fibers, or if the reaction fibers themselves effect a reorientation in the axis.

The relationship between reaction fibers and the orientation of branchlike axes does not seem to apply to the presence of reaction fibers in the smaller leaves of the Leguminosae studied (*Wisteria sinensis, Robinia pseudoacacia, Cercis canadensis, Caranga arborescens, Gleditsia triacanthos*). Reaction fibers were not only inconsistently distributed with respect to the upper side of horizontally positioned leaves and often positioned on opposite sides of the axis at a given level, but were also found in quantity in leaves that were hanging vertically. This circumstantial evidence suggests that reaction fibers are not influential in leaf orientation; developmental evidence would be necessary to substantiate such a conjecture. Active orientation, although apparently not mediated by reaction fibers, does occur in these leaves, as indicated by the great variation in the angle that different leaf axes make with the stem; it is probably controlled by the flexible, cylindrical pulvini, which lack reaction fibers. Pulvinal action is probably a more responsive mechanism of orientation than reaction-fiber contraction for these medium-sized leaves. The inconsistent distribution of reaction fibers with respect to gravity in these leaves, as well as the absence of any secondary orientation of the leaf axis that can be correlated with reaction-fiber distribution, suggests that their distribution might produce a balanced tension in the slender leaf axis (assuming that the fibers differentiate concurrently), which might help to provide a firm support for the leaf. In contrast to their apparent function in the secondary orientation of larger leaves in both the Leguminosae and the large-leaved species of the Meliaceae, this possible function of leaf reaction fibers in small-leaved leguminous species does not resemble the function of reaction fibers in branches.

The presence of reaction fibers in leaves provides another example of the independent and flexible relationship between tissues and organs in plants. In large compound leaves, most strikingly those of *Guarea glabra,* distribution of reaction fibers like that found in branches accompanies morphological modifications of the leaf into a branchlike structure. Conversely, in the small-leaved Leguminosae studied, the distribution of reaction fibers in the leaf axis is not similar to that in branches and may serve a unique function in the context of the morphology of typical leaves. In addition, the entire absence of reaction fibers in the branches and large compound leaves of many species exemplifies the flexible relationship between structure and function

in plants. The control of secondary orientation is evidently related to more than one anatomic structure.

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